

Scotland's Rural College

Speed breeding orphan crops

Chiurugwi, T; Kemp, S; Powell, W; Hickey, LT

Published in:
Theoretical and Applied Genetics

DOI:
[10.1007/s00122-018-3202-7](https://doi.org/10.1007/s00122-018-3202-7)

Print publication: 01/03/2019

Document Version
Peer reviewed version

[Link to publication](#)

Citation for pulished version (APA):
Chiurugwi, T., Kemp, S., Powell, W., & Hickey, LT. (2019). Speed breeding orphan crops. *Theoretical and Applied Genetics*, 132(3), 607-616. <https://doi.org/10.1007/s00122-018-3202-7>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Speed breeding orphan crops

Tinashe Chiurugwi¹, Stuart Kemp², Wayne Powell^{3*}, Lee T. Hickey^{4*}

¹ Independent Consultant, Yarrabilba, Queensland 4207, Australia

² PastureWise Pty Ltd, Cargerie, Victoria 3334, Australia

³ SRUC, Peter Wilson Building, King's Buildings, West Mains Road, Edinburgh EH9 3JG, UK

⁴ Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, St Lucia, Queensland 4072, Australia

*Corresponding authors:

Wayne Powell, email: wayne.powell@sruc.ac.uk, phone: +44 131 535 4001

Lee T Hickey, email: l.hickey@uq.edu.au, phone: +61 7 3365 4805

ORCID iDs:

TC: 0000-0002-5539-126X

WP: 0000-0002-5612-3398

LTH: 0000-0001-6909-7101

Keywords: orphan crops, speed breeding, diet diversity, food and nutrition security, micronutrients

Key message: This review explores how speed breeding protocols that hasten plant growth and development could be applied to shorten breeding cycles and accelerate research activities in orphan crops.

Authors' contribution: LTH and WP conceived and outlined the review; TC and WP contributed technical knowledge of breeding orphan crops; SK contributed concepts and technical knowledge for converting shipping containers into speed breeding capsules; LTH contributed technical knowledge of speed breeding; TC, SK, WP, and LTH wrote the manuscript.

Acknowledgements: We are grateful to Graeme Wright (Peanut Company of Australia) for providing a photograph of peanut plants growing under speed breeding conditions (Fig. 1a)

and Cathie Martin and Abhimanyu Sarkar (John Innes Centre) for providing a photograph of grass pea growing under speed breeding conditions (Fig. 1b). The authors would like to thank the Australian Research Council for support through an Early Career Discovery Research Award to Lee Hickey (DE170101296).

Conflict of interest: The authors declare that they have no conflict of interest.

Abstract

There is a growing need for the agri-food sector to sustainably produce larger quantities of higher-quality food, feed and fuel using fewer resources, within the context of changing agroclimatic conditions. Meeting this challenge will require the accelerated development and dissemination of improved plant varieties and substantial improvement of agricultural practices. Speed breeding protocols that shorten plant generation times can hasten breeding and research to help fulfil the ever-increasing demands. Global agri-food systems rely on a relatively small number of plant species; however, there are calls to widen the scope of globally-important crops to include orphan crops, which are currently grown and used by the world's poorest people or marketed as niche products for affluent consumers. Orphan crops can supply global diets with key nutrients, support economic development in the world's poorest regions, and bolster the resilience of the global agri-food sector to biotic and abiotic stresses. Little research effort has been invested in orphan crops, with farmers growing landraces that are sourced and traded through poorly structured market systems. Efforts are underway to develop breeding resources and techniques to improve orphan crops. Here, we highlight the current efforts and opportunities to speed breed orphan crops and discuss alternative approaches to deploy speed breeding in the less-resourced regions of the world. Speed breeding is a tool that, when used together with other multidisciplinary R&D approaches, can contribute to the rapid creation of new crop varieties, agricultural practices and products, supporting the production and utilisation of orphan crops at a commercial scale.

Introduction

Ensuring global food and nutrition security is an age-old challenge, which is being exacerbated by the accelerated population growth rates in poor and emerging economies, urbanisation, extreme and changing climates, the need to minimise the environmental impact of agricultural activities, and the competing demands for food, feed and fuel (Godfray et al. 2010; Alexandratos and Bruinsma 2012). Global agri-food systems depend on a small and decreasing number of plant and animal species and strains (Khoury et al. 2014); however, there are concerted efforts to incorporate orphan crops, plant species whose production and utilisation has been limited to a few regions or niche markets.

Orphan crops are comparatively underexploited or underutilised food plants characterised as having relatively low or no perceived economic importance or agricultural significance in advanced economies, meaning they receive relatively little research and development attention (Varshney et al. 2012; Sogbohossou et al. 2018). Orphan crops provide food and income for farmers in the poorest regions of the world, mainly in Africa, Asia, central and south America, and Oceania, where they are adapted to local conditions and act as important staples in local diets (Ebert 2014). Since most orphan crops have special traits (e.g., low glycaemic indices and high concentrations of micronutrients), they are not only important for nutritional security in poor communities, but are now being explored for improved and diverse diets in non-traditional and more affluent markets in both developing and advanced economies (Weinberger 2007).

Orphan crops are also important for supporting affordable, sustainable and diverse farming systems because they usually require less water than most global staples and can sometimes improve soils through nitrogen fixation and the incorporation of organic matter. Moreover, most orphan crops are hardy and can tolerate harsh conditions such as drought, frost, pests and disease. Orphan crops could therefore help protect world food supplies, particularly as challenges such as climate change, diseases and pests threaten global food crop monocultures. Worldwide, 90% of human calorific needs are supplied by only 20 species, with 60% of the global crop output coming from wheat (*Triticum aestivum*), maize (*Zea mays*), rice (*Oryza sativa*) and soya (*Glycine max*) (Massawe et al. 2016). In poor and

food-insecure regions of the world, however, the acreage devoted to orphan crops is often comparable to that of the major crop species (Tadele 2018).

A main production limitation for orphan crops is the poor genetic makeup of cultivated strains, which could be addressed by applying modern plant breeding techniques to develop superior cultivars and improve seed supply systems. Rapid advances in breeding and research can be achieved through shorter breeding cycles (i.e., the time between crossing and the selection of progeny to use as parents for the next cross) and a reduction in the number of cycles needed to generate new varieties. Recent advances in breeding techniques, including genetic engineering, genomic selection and doubled-haploid technology, have shortened breeding cycles and increased the rates of genetic gain in crops such as wheat, rice and maize (Hickey et al. 2017). These technologies can have an even greater impact if combined with speed breeding techniques, which enable rapid generation advancement by growing plant populations under controlled photoperiod and temperature regimes to hasten their growth and development (Li et al. 2018; Watson et al. 2018).

The rate of genetic gain in a breeding programme can be represented by the breeder's equation, a model of the expected change in a trait in response to selection (Lush 1943; Falconer and Mackay 1996; Lynch and Walsh 1998). The equation can be written as: $R = \frac{\delta_g \times i \times r}{L}$, where R is the change in the trait mean per year, δ_g is the amount of genetic variation within the population, i is the selection intensity, r is the selection accuracy, and L is the length of the breeding cycle. Based on this equation, speed breeding protocols can improve genetic gain in crop improvement programmes by increasing the number of plant generations cycled in one year, which can substantially reduce the length of the breeding cycle. This is particularly useful for crossing and line development prior to field evaluation.

Speed breeding protocols are also useful for synchronising the flowering of cultivated and wild individuals of orphan crop species, thus increasing the amount of variation in breeding populations and speeding up the attainment of breeding goals. Techniques for rapid cycling can include any combination of the following approaches: optimising the plant growth environment (e.g., plant density, photoperiod and temperature), genetic engineering targeting the flowering pathway, grafting juvenile plants to mature rootstocks, applying plant growth regulators and harvesting immature seed

(O'Connor et al. 2013; van Nocker and Gardiner 2014; Ceballos et al. 2017; Watson et al. 2018; Ghosh et al. 2018; Lulsdorf and Banniza 2018).

Modern breeding techniques are only beginning to be applied to orphan crops, and the benefits are expected to exceed those for most conventional crops (Varshney et al. 2012; Pazhamala et al. 2015; Kumar et al. 2016). Recent examples include the high-throughput genotyping of more than 100 orphan crops (Fox 2013), and the implementation of genomic selection in cassava (*Manihot esculenta*; Wolfe et al. 2017). Despite this progress, the limited ability to make the crosses needed for hybridisation and the time required for subsequent selfing to produce homozygous lines is a major bottleneck. This bottleneck exists because most orphan crops are still in the early stages of domestication, have long juvenile periods, suffer from asynchronous flowering across existing germplasm (hampering hybridisation and the transfer of traits of interest) and some species are vegetatively propagated. Speed breeding protocols will help address this limitation and enable the use of modern breeding methods; for example, the rapid development of recombinant inbred lines in a speed breeding system could facilitate rapid genomics-assisted breeding (O'Connor et al. 2013; Li et al. 2018).

The global acreage devoted to some orphan crops is increasing due to their adoption in advanced economies, for example, the increasing use of broad bean, lupin and lentil as rotation and break crops (Siddique et al. 2000; Amare et al. 2015). Because of this wider adoption, there is a need for the rapid development of special-use varieties and the introduction of traits that will facilitate production in new environments. The traits that are important to smallholder farmers in poorer parts of the world may not receive much attention during this wider adoption; therefore, the resources targeted at these traits must also be increased to accelerate their introduction into farmer-preferred varieties. Breeding better varieties also has the potential to increase the incomes of poor smallholder farmers by enabling them to access new and higher-value markets.

Several articles have documented and reviewed orphan crops, detailing their centres of origin, regions of production, special attributes, traditional and new uses, and breeding progress, amongst other things (Naylor et al. 2004; Nelson et al. 2004; Varshney et al. 2012; African Orphan Crops Consortium 2018; Tadele 2018). In this review, we explore the opportunities, challenges and tools required to apply speed breeding techniques to

promote synchronous flowering for crossing and increase the number of generations per year to accelerate orphan crop breeding and research. We also discuss potential delivery mechanisms to make speed breeding accessible to orphan crop breeding programmes worldwide.

Speed breeding orphan crops in practice

The following is a review of the application (actual and potential) of speed breeding to a selection of crops from the following groups: grasses and cereals, RTB crops, legumes and oilseeds, leafy vegetables and fruit trees (see Table 1 for examples). Later, we discuss a specific example of speed breeding in peanut (*Arachis hypogaea*).

[Table 1 here]

Cereals

Speed breeding protocols that employ extended photoperiods and controlled temperatures to accelerate growth and development have been developed for temperate cereals such as wheat and barley (*Hordeum vulgare*), enabling up to six generations per year (Watson et al. 2018). Most orphan grass and cereal crops are tropical short-day (SD) plants, however, and speed breeding protocols for these crops have yet to be developed. Rapid cycling protocols have been developed for some SD species such as *Amaranthus spp.* (Table 1) (Stetter et al. 2016; Joshi et al. 2018), with efforts underway to trial the amaranth protocol in the SD crop sorghum (*Sorghum bicolor*) at The University of Queensland in Australia. Growing SD species under long-day (LD), high-temperature conditions promotes vigorous vegetative growth, and a subsequent transfer to SD conditions induces flowering almost immediately. This technique has been used to help synchronise the flowering times of diverse germplasm and facilitate hybridisation in amaranth (Stetter et al. 2016).

Legumes and oilseeds

A number of protocols have been developed to shorten generation times in orphan legumes and oilseeds, including lupin (*Lupinus sp.*) (Croser et al. 2016), chickpea (*Cicer arietinum*) (Sethi et al. 1981; Watson et al. 2018), subterranean clover (*Trifolium subterraneum*) (Pazos-Navarro et al. 2017), lentil (*Lens culinaris*) and broad beans (*Vicia faba*) (Mobini et al. 2015; Lulsdorf and Banniza 2018) (see Table 1). The relatively higher interest in these crops is

probably because some of them are now entering mainstream agri-food systems and require more cost-efficient breeding programs capable of responding quickly to climate or disease challenges (Kole 2007; Pazos-Navarro et al. 2017).

Roots, tubers and bananas

Because these crops are clonally propagated, cultivated RTB crops lack diversity, and in some cases millions of people worldwide are dependent on a few clones (Heslop-Harrison and Schwarzacher 2007). This means that the food security and livelihoods of these people are vulnerable to disease and pest epidemics, the incidence and impact of which are expected to increase due to a number of biophysical and socioeconomic factors (Godfray et al. 2010; Sundström et al. 2014; Ehrlich and Harte 2015). Accelerated breeding will therefore be instrumental in introducing desired traits, particularly in response to new and devastating diseases, such as banana bacterial wilt and cassava brown streak disease.

The seeds of RTB crops are not typically important to farmers from an economic perspective. Most RTB crops are vegetatively propagated, with flowering in the field occurring either late (after several years of vegetative growth), rarely or only under special conditions. Making crosses in these crops during breeding programmes is therefore not trivial. Speed breeding protocols are yet to be developed for RTB crops, but there have been efforts to shorten the time to flowering as well as the flowering rate and predictability of many species (Wilson 1979; Ceballos et al. 2012; Jamnadass et al. 2015; Silva Souza et al. 2018). For RTBs and other clonally propagated crops, breeding programmes are aimed at producing elite clones for further testing and deployment. If genomics-assisted breeding approaches are used to estimate the breeding value of individual plants (as has been done in cassava; Wolfe et al. 2017), then speed breeding can be employed to make faster crosses and rapidly grow the progeny in preparation for the next round of breeding.

Leafy vegetables

Although most leafy vegetables have weedy growth habits and flower within 30–50 days of sowing, speed breeding protocols could synchronise flowering among the diverse germplasm used in breeding programmes. A speed breeding approach could be used to induce flowering in late-flowering or recalcitrant lines, and to accelerate the development and introduction of new varieties. A speed breeding protocol that achieves some of these

objectives has already been developed for amaranth (Stetter et al. 2016) (Table 1). New varieties are desperately needed because most orphan leafy vegetable crops (like other orphan crops) are still in the early stages of domestication. Key breeding objectives for leafy vegetables include pest and disease resistance and intra-specific uniformity in the harvested foliage and other products; for example, in amaranth, resistance to white rust (*Albugo bliti*) is a key trait (Wang and Ebert 2012), as is the combined high quality and quantity of foliage and grain yields (Dinssa et al. 2018).

Fruit trees

For most fruit trees, flowering occurs after a juvenile phase, which can range from a few years to more than twenty years (Korbo et al. 2013). Efforts to accelerate fruit tree breeding have therefore mainly focused on reducing the juvenile period, with some reports of protocols that promote such vigorous vegetative growth that flowering occurs within a fraction of the normal time; for example, in ten months instead of five years for apple (*Malus × domestica*) (van Nocker and Gardiner 2014) and two years instead of seven in chestnut (*Castanea sativa*) (Baier et al. 2012). The main challenge with speed breeding tree crops is that there is a need for extra resources or protocol modifications to prevent the plants from becoming too tall and difficult to manage in the confines of controlled environment facilities. Techniques for breaking seed dormancy have also proven valuable for reducing the seed-to-seed interval in some tree species (van Nocker and Gardiner 2014).

Table 1: The generation time, photoperiod response and status of speed breeding in ten orphan crops from five categories: cereals; roots, tubers and bananas; legumes and oilseeds; leafy vegetables; and fruit trees.

| Crop | Field generation time (days) | Photoperiod response | Speed breeding protocol |
|--|------------------------------|------------------------------|---|
| Cereals | | | |
| Finger millet (<i>Eleusine coracana</i>) | 80–100 | SD ¹ | Not yet developed |
| Sorghum (<i>Sorghum bicolor</i>) | 130–150 | SD | Not yet developed |
| Roots, tubers and bananas | | | |
| Cassava (<i>Manihot esculenta</i>) | 640–730 | LD ² /day neutral | Not yet developed; LD and cool temperatures induce early flowering (Keating et al. 1982) |
| Banana/plantain (<i>Musa spp.</i>) | 180–275 | Day neutral | Not yet developed |
| Legumes and oilseeds | | | |
| Chickpea (<i>Cicer arietinum</i>) | 90–160 | Quantitative LD | Watson et al. (2018) - 22-h LD - 22/17°C (day/night) - Four to six generations per year |
| Peanut (<i>Arachis hypogaea</i>) | 145 | SD/day neutral | O'Connor et al. (2013) - Continuous light - 28/17°C (day/night) - Three generations per year |
| Leafy vegetables | | | |
| Amaranth (<i>Amaranthus spp.</i>) | 180 | Obligate SD | Stetter et al. (2016) - 8-h SD |

| Crop | Field generation time (days) | Photoperiod response | Speed breeding protocol |
|---|------------------------------|----------------------|--------------------------------------|
| | | | - 30°C - Six generations per year |
| Jute mallow (<i>Corchorus olitorius</i>) | 40–60 | Quantitative SD | Not yet developed |
| Fruit trees | | | |
| Baobab (<i>Adansonia spp.</i>) | 5800–8400 | Day neutral | Not yet developed |
| Desert date (<i>Balanites aegyptiaca</i>) | 1800–2600 | Day neutral | Not yet developed |

¹SD – short day

²LD – long day

Common challenges

Facilities, equipment and personnel

A main challenge in implementing speed breeding is the precise control of the growing conditions (particularly the photoperiod, temperature and humidity) and disease or pest infestations. This is particularly important for orphan crops, as most breeding programmes for these crops operate in the poorest regions of the world, with limited or unreliable access to electricity and other resources necessary to operate speed breeding facilities.

Additionally, the selection of key traits during the rapid advancement phase of the breeding cycle may require specialist equipment that is not readily accessible to orphan crop breeders. Further, most orphan crop breeding programmes have poor access to reliable field trial facilities and appropriately skilled personnel, and have limited opportunities for training and continuous professional development. This will complicate the deployment and full exploitation of orphan crop speed breeding. Projects are underway to try to address the issues with facilities, equipment and personnel in orphan crop breeding, including various CGIAR initiatives, the Next Generation Cassava project (NextGen Cassava 2018) and the African Orphan Crop Consortium (African Orphan Crops Consortium 2018), but there is still a need for a special emphasis on speed breeding systems within these initiatives.

Unmanned aerial vehicles (drones) fitted with cameras and other sensors now allow cost-effective, high-throughput, large-scale assessments of plant populations in the field (Shi et al. 2016; Yang et al. 2017). Drone-assisted phenotyping is now cheap and cost-effective (Yang et al. 2017; Reynolds et al. 2018) and should soon be available to researchers in low-income countries. Linking speed breeding with high-throughput phenotyping tools in orphan crops provides the capacity to assess plants based on selection indices incorporating multiple traits of interest and to rapidly generate new cultivars.

Cost

Speed breeding can be expensive, and the number of crosses and the population sizes under evaluation are often limited by the size and cost of running a suitable facility. Combining speed breeding with other modern breeding techniques, such as genomics-assisted breeding to take advantage of established marker-trait associations, should help address this challenge by focussing resources on plants that are most likely to contribute to

the breeding objectives (Li et al. 2018). Combining speed breeding with improved field trials will also ensure that researchers target only those parts of the breeding programme that would benefit from acceleration, such as the parental crossing process in clonally propagated crops or those with long juvenile periods, or the production of elite inbred lines following hybridisation (Li et al. 2018). More than half the cost of speed breeding systems goes towards lighting and temperature control (O'Connor et al. 2013). It is possible to reduce this cost using energy efficient lighting (such as LED) and air conditioning (such as inverter-based) systems, as well as using solar power to supplement electricity and gas from the national grid (Ghosh et al. 2018).

Despite the extra cost (which was about 100% more than using standard conditions for one peanut protocol; O'Connor et al. 2013), speed breeding is still a reasonable choice for the rapid advancement of early-generation breeding materials in poorly resourced breeding programmes, which have limited access to suitable land, equipment and personnel (O'Connor et al. 2013). Moreover, linking the breeding programmes to systems for the rapid commercialisation of new varieties would enable these extra breeding costs to be recouped (Collard et al. 2017).

Example: speed breeding peanut

Speed breeding has been applied to shorten the time it takes to develop new breeding lines for use in breeding programmes, field testing prior to release as new varieties, or participatory appraisal by farmers (Fig. 1, Fig. 2). The objectives and protocols will depend on the crop being bred and the levels and focus of current research and breeding investment; for example, whether speed breeding is being used to accelerate domestication, correct traits or as part of existing pre-breeding or breeding programmes.

Speed breeding protocols have been successfully used to develop commercial varieties of peanut (Fig. 1a) (O'Connor et al. 2013) and chickpea (Gaur et al. 2007). Protocols have also been developed for grass pea (*Lathyrus sativus*; Fig. 1b), lentil and quinoa to expedite breeding and research, which could soon lead to new varieties (Mobini et al. 2015; Ghosh et al. 2018; Lulsdorf and Banniza 2018).

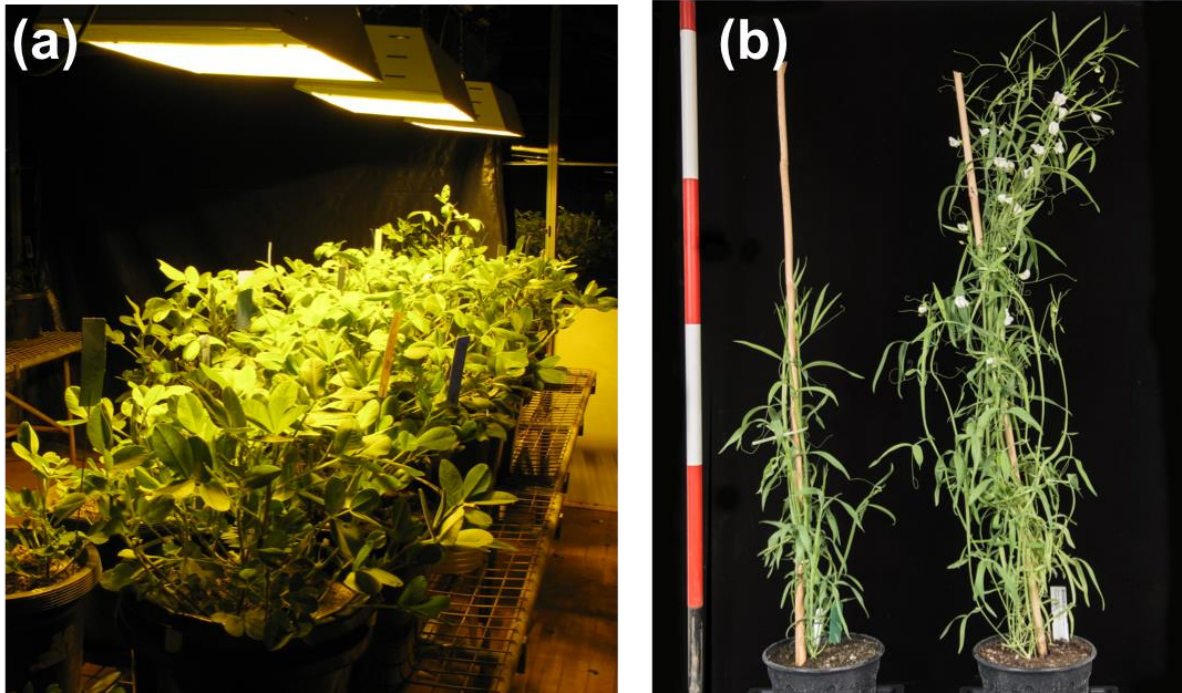


Fig. 1 Speed breeding has been applied to shorten generation time in many crop species. (a) F_2 peanut (*Arachis hypogaea*) plants growing under speed breeding conditions, which reduced the generation time from 145 days to 89 days (O'Connor et al. 2013). (b) Grass pea (*Lathyrus sativus*) at 35 days after sowing, showing accelerated plant growth and development under speed breeding (22-h photoperiod, right) in comparison with standard LD conditions (16-h photoperiod, left).

In peanut, speed breeding (under continuous light and a 28/17°C day/night temperature regime) was used to accelerate the development of elite lines for further testing in the field or for use as new parents (O'Connor et al. 2013). O'Connor et al. (2013) carried out parental crosses and grew F_1 plants in the field, and then successfully used speed breeding to inbreed the F_2 , F_3 and F_4 generations within 12 months. This could drastically reduce the time between the initial crosses and varietal release from 10–15 years to 6–7 years. If parental crosses and the screening and inbreeding of the F_1 generation are also carried out under speed breeding conditions, elite F_5 lines could be developed more than twice as rapidly as using conventional breeding (within 20 months instead of 54 months), and 10 months faster than conventional breeding including a winter nursery (Fig. 2). To take full advantage of this accelerated generation advancement, more facilities and

resources may be required to allow the elite lines from speed breeding phase to be taken into the next stage of the breeding or research programme as soon as they are ready, which would be within one month for peanut.

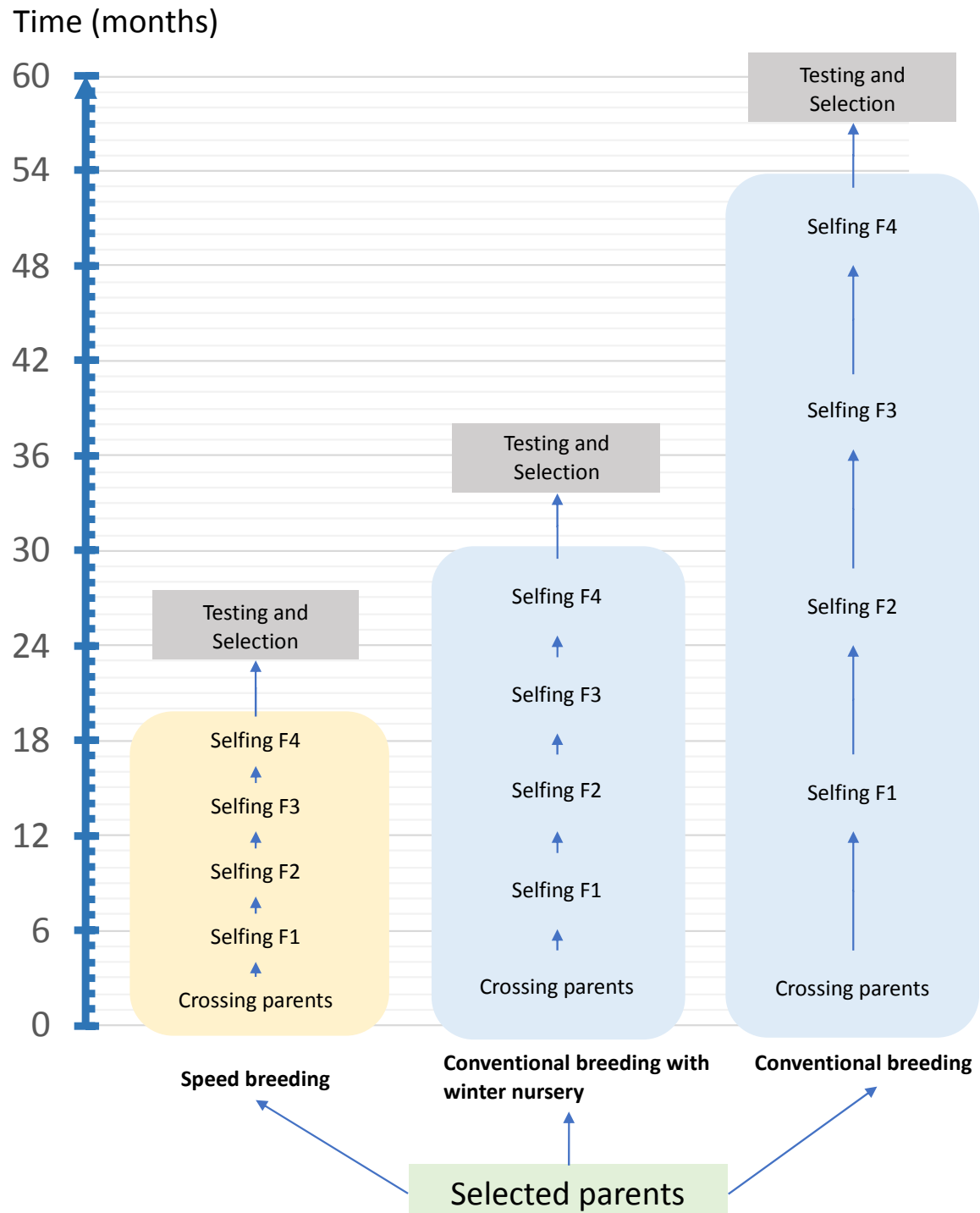


Fig. 2 Schematic comparison of time required to develop elite lines from selected parents of peanut using speed breeding (20 months, three generations/year), conventional breeding

with a winter nursery (30 months, two generations/year) and conventional breeding (54 months, one generation/year) (adapted from O'Connor et al. 2013).

Prospects for application

Delivering speed breeding in orphan crops requires standardised, simplified, customisable and affordable approaches and techniques that can be used by orphan crop breeding programmes. While different crop species and breeding objectives will require customised speed breeding protocols, several key components of these protocols can be evaluated for local use to accelerate orphan crop improvement. These components include guidelines on growth media; lighting, temperature and humidity regimes; phenotyping; accelerated germination; and early harvesting (Watson et al. 2018; Ghosh et al. 2018). Below we discuss two alternative approaches that could be used to deploy orphan crop speed breeding: 1) the development and distribution of affordable speed breeding capsules and 2) the establishment of speed breeding centres.

Speed breeding capsules

Controlled environment cabinets and glasshouse facilities for plant research are typically expensive. This can be a major barrier to the adoption of speed breeding in many crop improvement programmes. There are many reports of hydroponic crop production in disused shipping containers or custom-built containers made of steel and composite material by amateur farmers around the world, including in Kenya and Nigeria (BBC 2018). Some indoor farming companies (for example, Modular Farms, Cropbox and Podponics in the USA and Australia) produce containers suitable for commercial-scale agricultural production. The primary focus of these efforts is to produce crops (mainly high-value herbs and leafy vegetables) in any location at any time of the year, grown closer to the point of consumption while using less land (about 99% less) and other resources (such as water and agrochemicals) than field-grown crops (CropBox 2018). Shipping containers can be retrofitted with multi-tier greenhouse benches, hydroponic systems, lighting and air conditioning for about 25 000 USD (Saenz 2011), while custom-built capsules will cost a little more. Capsules can be shipped anywhere in the world, provided there is access to an appropriate electricity and water supply.

In a similar fashion, speed breeding capsules can be built out of disused refrigerated shipping containers fitted with temperature and light controls, irrigation systems and greenhouse benches (Fig. 3). Since refrigerated containers are insulated and have slotted floors with drainage ports at either end, greenhouse benches may not be necessary for growing tall plants, which can be placed directly on the floor. The use of height adjustable LED lights improves the flexibility of the capsule, accommodating plants of different height while managing the light intensity at the canopy level. In warm climates, heat from the lights can be exhausted directly through vents in the walls of the container, while in cooler climates the heat generated by the lights can be retained to assist with heating. Ideally, the bulk of the electricity would be supplied from an attached solar power system. Such a capsule would cost much less than the hydroponic systems described above, and could be produced to specification anywhere in the world and shipped to local breeding programmes.

To further reduce speed breeding start-up costs and make the capsules more accessible to poorly-resourced breeding programmes, the key components of the capsules (light fittings, temperature controls, solar power system and collapsible greenhouse benches) could be deployed in 'kit' form. These components could then be fitted to local containers (following specific instructions) and the speed breeding capsules could be assembled in situ. The delivery of the capsule system would ideally be packaged with training on how to grow healthy plants and options for integrating the tool into existing breeding activities. Deploying speed breeding capsules will empower local breeders to carry out and customise the protocols, giving them ownership of the facilities and their speed breeding applications, which is important for future sustainability and further development.

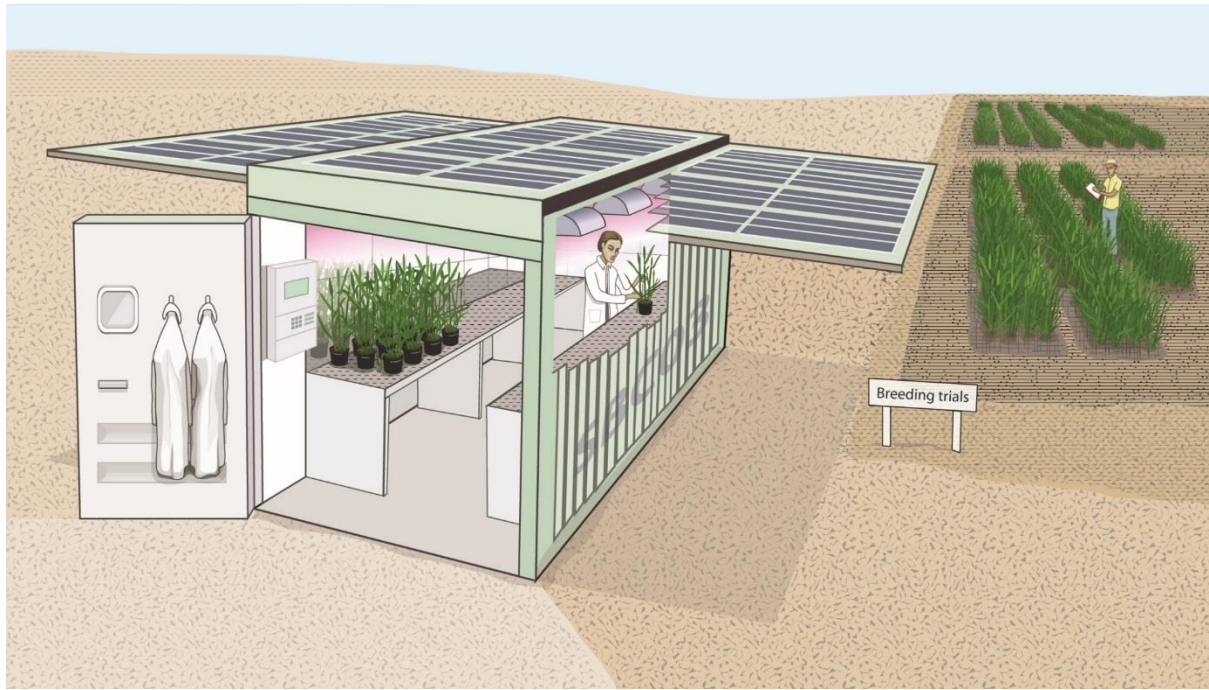


Fig. 3 Artist's impression of a speed breeding capsule made from a disused refrigerated shipping container and deployed for accelerated orphan crop breeding.

Speed breeding centres

An alternative approach to deploying speed breeding systems would be to develop centres with a regional or crop group focus, working in conjunction with existing partners to provide access to speed breeding facilities for orphan crop scientists. The focus of the speed breeding centres would be service provision, meaning they would offer a trait integration service and train scientists in the application of speed breeding and other modern breeding techniques. The trait integration service (incorporating other cutting-edge breeding techniques) would accelerate the transfer or stacking of traits into preferred orphan crop germplasm. The speed breeding centres would have large speed breeding facilities (greenhouses and controlled environment rooms) using low-cost components (such as LED lighting and solar power) and would be designed to handle a range of crops. The ideal hosting partners for the centres would be equipped, co-located or working closely with a facility that provides genotyping services and performs ongoing orphan crop breeding and research. This would help address phytosanitary handling issues, including plant quarantine and other matters relating to the movement of seed and plant material.

Examples of well-positioned partners for potential speed breeding centres include the following: the West Africa Centre for Crop Improvement (Ghana), the BeCa-ILRI Hub (Kenya), the World Vegetable Center (Taiwan), the African Orphan Crops Consortium (Kenya), Crops for the Future (Malaysia), the Global Pulse Confederation (UAE) and the CGIAR Centres and Research Programmes (worldwide). Scientists at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the International Institute of Tropical Agriculture (IITA) and the International Center for Agricultural Research in the Dry Areas (ICARDA) (CGIAR centres) have indicated a desire to develop speed breeding facilities to accelerate breeding for their mandated crops. Some of these centres already use various approaches to induce flowering or accelerate plant growth and development in orphan crops (Ceballos et al. 2017). If they manage to gather the resources to develop these facilities, they would immensely benefit a number of breeding programmes for high-priority orphan crops across Africa, Asia and the Middle East.

Conclusions

It is important to note that, as with any breeding technology, speed breeding has limitations and can only be used to accelerate those parts of a breeding or research programme that would benefit from accelerated generation advancement. For maximum benefit, orphan crop researchers will need guidance on identifying these phases and the best protocols by which to accelerate them.

Speed breeding must therefore be integrated with other breeding techniques as well as cost-efficient high-throughput genotyping and phenotyping to speed up the generation, testing and commercial release of orphan crop varieties. In particular, field testing and the involvement of farmers in the testing and evaluation of elite lines will be integral to accelerating the development and dissemination of improved varieties. This is particularly important for orphan crops, which have nuanced traits for integration into local farming systems, diets and traditions. Thorough and reliable field testing coupled with client-oriented innovation, which considers the entire value chain (from seed supply to consumers) to facilitate the development and uptake of improved varieties, will therefore be essential for the speed breeding of orphan crops.

While our focus here has been speed breeding orphan crops of great importance to resource-poor communities, the concepts and principles can also be applied to the improvement of other crops that have not received much research and breeding attention or are in the early stages of domestication in more advanced economies. These include native grasses, legumes and shrubs used for livestock forage (Nichols et al. 2012; Mitchell et al. 2015; Pazos-Navarro et al. 2017) and plants that have found new uses as energy or medicinal crops, such as *Miscanthus spp.* (Clifton-Brown et al. 2017). Therefore, speed breeding can be integrated with multiple disciplines, concepts and resources to rapidly improve orphan crops and bring them to the forefront of the quest for a well-nourished world population, in the context of unpredictable environmental and socioeconomic conditions.

References

- African Orphan Crops Consortium (2018) African Orphan Crops Consortium.
<http://africanorphancrops.org/>. Accessed 3 Aug 2018
- Alexandratos N, Bruinsma J (2012) World agriculture towards 2030/2050: the 2012 revision.
FAO, Rome
- Amare E, Mouquet-Rivier C, Servent A, et al (2015) Protein Quality of Amaranth Grains
Cultivated in Ethiopia as Affected by Popping and Fermentation. *Food Nutr Sci*. doi:
10.4236/fns.2015.61005
- Baier KM, Maynard C, Powell W (2012) Early flowering in chestnut species induced under
high dose light in growth chambers. *J Am Chestnut Found* 26:8–10
- BBC (2018) Nigerian entrepreneur: “We’re farming in a shipping container.”
<https://www.bbc.com/news/av/business-42919553/nigerian-entrepreneur-we-re-farming-in-a-shipping-container>. Accessed 7 Aug 2018
- Ceballos H, Hershey C, Becerra-López-Lavalle LA (2012) New Approaches to Cassava
Breeding. *Plant Breed Rev* 36:427–504. doi: 10.1002/9781118358566.ch6
- Ceballos H, Jaramillo JJ, Salazar S, et al (2017) Induction of flowering in cassava through
grafting. *J Plant Breed Crop Sci* 9:19–29
- Clifton-Brown J, Hastings A, Mos M, et al (2017) Progress in upscaling *Miscanthus* biomass
production for the European bio-economy with seed-based hybrids. *GCB Bioenergy*.
doi: 10.1111/gcbb.12357
- Collard BCY, Beredo JC, Lenaerts B, et al (2017) Revisiting rice breeding methods –
evaluating the use of rapid generation advance (RGA) for routine rice breeding. *Plant
Prod Sci* 20:337–352. doi: 10.1080/1343943X.2017.1391705
- CropBox (2018) A new, smarter way to farm. <http://cropbox.co>. Accessed 15 Aug 2018
- Croser JS, Pazos-Navarro M, Bennett RG, et al (2016) Time to flowering of temperate pulses
in vivo and generation turnover in vivo--in vitro of narrow-leaf lupin accelerated by low
red to far-red ratio and high intensity in the far-red region. *Plant Cell, Tissue Organ Cult*
127:591–599. doi: 10.1007/s11240-016-1092-4

- Dinssa FF, Yang R-Y, Ledesma DR, et al (2018) Effect of leaf harvest on grain yield and nutrient content of diverse amaranth entries. *Sci Hortic (Amsterdam)* 236:146–157. doi: <https://doi.org/10.1016/j.scienta.2018.03.028>
- Ebert AW (2014) Potential of underutilized traditional vegetables and legume crops to contribute to food and nutritional security, income and more sustainable production systems. *Sustain.* doi: 10.3390/su6010319
- Ehrlich PR, Harte J (2015) Opinion: To feed the world in 2050 will require a global revolution. *Proc Natl Acad Sci* 112:14743–14744
- Falconer DS, Mackay TFC (1996) *Introduction to quantitative genetics*. Longman, New York, NY
- Fox JL (2013) Mars collaborates to sequence Africa's neglected food crops. *Nat Biotechnol* 31:867
- Gaur P, Samineni S, Laxmipathi Gowda C, Rao B V (2007) Rapid generation advancement in chickpea. *SAT eJournal* 3:1–3
- Ghosh S, Watson A, Gonzalez-Navarro OE, et al (2018) Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. *bioRxiv* 369512. doi: <https://doi.org/10.1101/369512>
- Godfray HCJ, Beddington JR, Crute IR, et al (2010) Theme Issue 'Food security: feeding the world in 2050.' *Philos Trans R Soc Biol Sci* 365:2765–3097
- Heslop-Harrison JS, Schwarzacher T (2007) Domestication, Genomics and the Future for Banana. *Ann Bot* 100:1073–1084
- Hickey JM, Chiurugwi T, Mackay I, et al (2017) Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nat Genet* 49:1297–1303
- Jamnadass RH, McMullin S, Iiyama M, et al (2015) Understanding the Roles of Forests and Tree-based Systems in Food Provision. In: Vira B, Wildburge C, Mansourian S (eds) *Forests, trees and landscapes for food security and nutrition: a global assessment report*. International Union of Forest Research Organizations (IUFRO), Viena, pp 25–50
- Joshi DC, Sood S, Hosahatti R, et al (2018) From zero to hero: the past, present and future of grain amaranth breeding. *Theor Appl Genet.* doi: 10.1007/s00122-018-3138-y

- Keating BA, Evenson JP, Fukai S (1982) Environmental effects on growth and development of cassava (*Manihot esculenta* Crantz.) I. Crop development. *F Crop Res* 5:271–281. doi: [https://doi.org/10.1016/0378-4290\(82\)90030-2](https://doi.org/10.1016/0378-4290(82)90030-2)
- Khoury CK, Bjorkman AD, Dempewolf H, et al (2014) Increasing homogeneity in global food supplies and the implications for food security. *Proc Natl Acad Sci* 111:4001–4006
- Kole C (2007) Pulses, sugar and tuber crops. Springer, Berlin, Heidelberg
- Korbo A, Kjær ED, Sanou H, et al (2013) Breeding for high production of leaves of baobab (*Adansonia digitata* L) in an irrigated hedge system. *Tree Genet Genomes*. doi: 10.1007/s11295-013-0595-y
- Kumar V, Khan AW, Saxena RK, et al (2016) First-generation HapMap in *Cajanus* spp. reveals untapped variations in parental lines of mapping populations. *Plant Biotechnol J* 14:1673–1681. doi: 10.1111/pbi.12528
- Li H, Rasheed A, Hickey LT, He Z (2018) Fast-Forwarding Genetic Gain. *Trends Plant Sci* 23:184–186. doi: 10.1016/j.tplants.2018.01.007
- Lulsdorf MM, Banniza S (2018) Rapid generation cycling of an F2 population derived from a cross between *Lens culinaris* Medik. and *Lens ervoides* (Brign.) Grande after aphanomyces root rot selection. *Plant Breed* 137:486–491. doi: 10.1111/pbr.12612
- Lush JL (1943) Animal Breeding Plans. The Iowa State College Press, Ames, IA
- Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, MA
- Massawe F, Mayes S, Cheng A (2016) Crop Diversity: An Unexploited Treasure Trove for Food Security. *Trends Plant Sci* 21:365–368. doi: 10.1016/j.tplants.2016.02.006
- Mitchell ML, Norman HC, Whalley RDB (2015) Use of functional traits to identify Australian forage grasses, legumes and shrubs for domestication and use in pastoral areas under a changing climate. *Crop Pasture Sci* 66:71–89
- Mobini SH, Lulsdorf M, Warkentin TD, Vandenberg A (2015) Plant growth regulators improve in vitro flowering and rapid generation advancement in lentil and faba bean. *Vitr Cell Dev Biol - Plant* 51:71–79. doi: 10.1007/s11627-014-9647-8

- Naylor RL, Falcon WP, Goodman RM, et al (2004) Biotechnology in the developing world: a case for increased investments in orphan crops. *Food Policy* 29:15–44. doi: <https://doi.org/10.1016/j.foodpol.2004.01.002>
- Nelson RJ, Naylor RL, Jahn MM (2004) The role of genomics research in improvement of “orphan” crops. *Crop Sci* 44:1901–1904. doi: 10.2135/cropsci2004.1901
- NextGen Cassava (2018) Next Generation Cassava Breeding Project. <http://www.nextgencassava.org/index.html>. Accessed 3 Aug 2018
- Nichols PGH, Revell CK, Humphries AW, et al (2012) Temperate pasture legumes in Australia - Their history, current use, and future prospects. *Crop Pasture Sci* 63:691–725. doi: 10.1071/CP12194
- O’Connor DJ, Wright GC, Dieters MJ, et al (2013) Development and Application of Speed Breeding Technologies in a Commercial Peanut Breeding Program. *Peanut Sci*. doi: 10.3146/PS12-12.1
- Pazhamala L, Saxena RK, Singh VK, et al (2015) Genomics-assisted breeding for boosting crop improvement in pigeonpea (*Cajanus cajan*). *Front Plant Sci* 6:50. doi: 10.3389/fpls.2015.00050
- Pazos-Navarro M, Castello M, Bennett RG, et al (2017) In vitro-assisted single-seed descent for breeding-cycle compression in subterranean clover (*Trifolium subterraneum* L.). *Crop Pasture Sci* 68:958–966. doi: 10.1071/CP17067
- Reynolds D, Baret F, Welcker C, et al (2018) What is cost-efficient phenotyping? Optimizing costs for different scenarios. *Plant Sci*. doi: <https://doi.org/10.1016/j.plantsci.2018.06.015>
- Saenz A (2011) Transforming Shipping Containers Into Local Farms – PodPonics Brings Produce to the City. In: Singul. Hub. <https://singularityhub.com/2011/08/30/transforming-shipping-containers-into-local-farms-podponics-brings-produce-to-the-city/#sm.000100v3z66e9fdyt062k15j3s238>. Accessed 7 Aug 2018
- Sethi SC, Byth DE, Gowda CLL, Green JM (1981) Photoperiodic response and accelerated generation turnover in chickpea. *F Crop Res* 4:215–225. doi: 10.1016/0378-

- Shi Y, Thomasson JA, Murray SC, et al (2016) Unmanned Aerial Vehicles for High-Throughput Phenotyping and Agronomic Research. *PLoS One* 11:e0159781
- Siddique KHM, Brinsmead RB, Knight R, et al (2000) Adaptation of chickpea (*Cicer arietinum* L.) and faba bean (*Vicia faba* L.) to Australia. In: Knight R (ed) *Linking Research and Marketing Opportunities for Pulses in the 21st Century: Proceedings of the Third International Food Legumes Research Conference*. Springer Netherlands, Dordrecht, pp 289–303
- Silva Souza L, Diniz RP, Neves R de J, et al (2018) Grafting as a strategy to increase flowering of cassava. *Sci Hortic (Amsterdam)* 240:544–551. doi: 10.1016/j.scienta.2018.06.070
- Sogbohossou EOD, Achigan-Dako EG, Maundu P, et al (2018) A roadmap for breeding orphan leafy vegetable species: a case study of *Gynandropsis gynandra* (Cleomaceae). *Hortic Res* 5:2. doi: 10.1038/s41438-017-0001-2
- Stetter MG, Zeitler L, Steinhaus A, et al (2016) Crossing Methods and Cultivation Conditions for Rapid Production of Segregating Populations in Three Grain Amaranth Species. *Front Plant Sci*. doi: 10.3389/fpls.2016.00816
- Sundström JF, Albiñá A, Boqvist S, et al (2014) Future threats to agricultural food production posed by environmental degradation, climate change, and animal and plant diseases -- a risk analysis in three economic and climate settings. *Food Secur* 6:201–215. doi: 10.1007/s12571-014-0331-y
- Tadele Z (2018) *African Orphan Crops under Abiotic Stresses: Challenges and Opportunities*. Scientifica (Cairo). doi: 10.1155/2018/1451894
- van Nocker S, Gardiner SE (2014) Breeding better cultivars, faster: applications of new technologies for the rapid deployment of superior horticultural tree crops. *Hortic Res* 1:14022. doi: 10.1038/hortres.2014.22
- Varshney RK, Ribaut J-M, Buckler ES, et al (2012) Can genomics boost productivity of orphan crops? *Nat Biotechnol* 30:1172–1176. doi: 10.1038/hortres.2014.22
- Wang S tai, Ebert A (2012) Breeding of leafy amaranth for adaptation to climate change. In: *Regional Symposium on High Value Vegetables in Southeast Asia: Production, Supply*

- and Demand (SEAVEG2012). VRDC – The World Vegetable Center, Chiang Mai
- Watson A, Ghosh S, Williams MJ, et al (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. *Nat Plants*. doi: 10.1038/s41477-017-0083-8
- Weinberger K (2007) Are Indigenous vegetables underutilized crops? Some evidence from eastern Africa and South East Asia. *Acta Hort* 752:29–34. doi: 10.17660/ActaHortic.2007.752.1
- Wilson JE (1979) Promotion of flowering and production of seed in cocoyam (*Xanthosoma* and *Colocasia*). In: 5th Intern. Symp. on Trop. Root Crops held in Manila, Philippines. September. pp 17–21
- Wolfe MD, Del Carpio DP, Alabi O, et al (2017) Prospects for Genomic Selection in Cassava Breeding. *Plant Genome*. doi: 10.3835/plantgenome2017.03.0015
- Yang G, Liu J, Zhao C, et al (2017) Unmanned Aerial Vehicle Remote Sensing for Field-Based Crop Phenotyping: Current Status and Perspectives. *Front Plant Sci*. doi: 10.3389/fpls.2017.01111